

ROLE OF LIVESTOCK AND BLACK-TAILED JACKRABBITS IN CHANGING ABUNDANCE OF *KOCHIA AMERICANA*¹

William R. Clark² and Frederic H. Wagner³

ABSTRACT.—Historical accounts and matched photographs indicate sharp decline of once-abundant *Kochia americana* in eastern Great Basin vegetation since the early 1900s, most of the decline by the late 1950s. Exclosure data show further decline from 1957 to 1973, then some increase between 1970 and 1973 and 1976 and 1981. Utah sheep numbers, at maximum from 1925 to 1940 and declining steadily to the 1970s, may have induced the long-term changes. Black-tailed jackrabbits (*Lepus californicus*), could not have induced vegetation decline, but could have added to livestock pressure and abetted the trend. In 1972, rabbits near a cyclic high were indirectly estimated to completely utilize *K. americana* in Curlew Valley, northwestern Utah. In 1976–1977 at rabbit low, direct measurements show 4%–18% of plants browsed by late summer, about 30%–50% of herbage removed from browsed plants. The latter rose to 45%–82% by end of winter. Late-summer percent browsed may have risen slightly (11%–21%) in 1980–1981 at next rabbit high. Increase in *K. americana* density from 1973 to 1976, then a slight decrease from 1976 to 1980, suggests fluctuating *K. americana* abundance induced by rabbit browsing, superimposed on long-term *K. americana* decline and recovery.

This paper presents data on the degree to which black-tailed jackrabbits (*Lepus californicus*) utilize the chenopodiaceous half-shrub *Kochia americana* in the salt-desert shrub vegetation of western Utah and explores the role of jackrabbits and livestock in the historic changes of abundance reported for this species. Various called “white sage” (Kearny et al. 1914), “brown sage” (Esplin et al. 1937), “grey molly” (Stewart et al. 1940), and “desert molly” (Cook 1961) by earlier authors and generally referred to as *Kochia vestita*, this halophytic suffrutescent half-shrub typically reaches heights of 5–20 cm. Its unbranched, vertical stems lignify and die each fall to be replaced by new spring growth rising from the root crown.

Kochia americana and other species of similar stature form a mosaic of vegetation types in the glacial Lake Bonneville basin, the patchwork of simple or monotypic communities reflecting variations in microtopography, salinity, and other soil variables. Historically, the species grew in extensive, nearly monotypic stands interdigitating with big sagebrush (*Artemisia tridentata*) at slightly higher elevations and merging with shadscale (*Atriplex confertifolia*) at its lower edge (Kearney et al. 1914). Alternatively, it grew and continues today as a co-dominant

with shadscale, or with greasewood (*Sarcobatus vermiculatus*) at still lower elevations.

The species has moderate forage value for sheep (Esplin et al. 1937, Cook and Stoddart 1953, Clarke and West 1969) and is preferred by black-tailed jackrabbits (Clark 1979, 1981, Westoby 1980). Several observers (e.g., Cook 1961, Rogers 1980) have reported sharp declines in *K. americana* abundance and distribution between the early 1900s and the 1950–1970s. These declines may be part of the more general, grazing-induced vegetation changes occurring over this same period (Kearny et al. 1914, Christensen and Johnson 1964, Holmgren and Hutchings 1972, Rogers 1980). More recently, our own observations indicate some increase in *K. americana* in the past decade or so. This paper addresses this history of changes in *K. americana* and possible herbivorous causation.

METHODS

Study Area

Measurements of *K. americana* density and biomass, utilization rates by jackrabbits, censuses of jackrabbits, and certain earlier studies to which we will refer were carried out in

¹Journal Paper J-10797 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project 2401.

²Department of Animal Ecology, Iowa State University, 124 Science II, Ames, Iowa 50011.

³Ecology Center, Utah State University, Logan, Utah 84322.

the Utah portion of 3300 km² Curlew Valley. The valley lies north of the Great Salt Lake in northwestern Utah and southern Idaho. Valley floor elevations range from 1585 to 1280 m, sloping toward the lake. A few isolated hills (maximum elevation ca 1585 m) occur in the study area. The climate, characteristic of the Great Basin Desert, has annual precipitation ranging from 180 to 420 mm, mostly as winter snow. Mean monthly temperatures range from -7 C in January to 23 C in July. Four major vegetation zones occur along the elevational gradient, including those dominated by Utah juniper (*Juniperus osteosperma*), big sagebrush, shadscale, and greasewood.

Although in earlier years *K. americana* occurred in a mosaic of pure stands and sagebrush patches in Curlew Valley (Cook 1961), it is found largely in association with shadscale and greasewood today. In the shadscale type, *K. americana* occurs as scattered individuals and as a near co-dominant with shadscale. In greasewood, it reaches its largest form, often under the greasewood canopy, but also scattered in the interspaces between the dominant shrubs. Both vegetation types include variable amounts of squirreltail grass (*Sitanion hystrix*), halogeton (*Halogeton glomeratus*), peppergrass (*Lepidium perfoliatum*), and tansy-mustard (*Descurainia* spp.).

Vegetation Measurements

In April 1976 two 1-ha livestock-proof reference areas were established in the valley to measure jackrabbit use of *K. americana*, one in the shadscale type, one in greasewood. Corners of 24 2 × 8 m plots were randomly located within each enclosure.

Kochia americana plants were sampled in these areas in June at approximate peak standing crop (Shinn et al. 1975) in 1976-1977, in August or September in these years plus 1980, and in February 1977 and 1978. Two measures of jackrabbit use were taken. The first, "percent removal," was the percentage of standing crop removed from *K. americana* plants that had been browsed. Jackrabbits waste much of the plants on which they browse (Currie and Goodwin 1966, Shoemaker et al. 1976). Cut stems and

wasted material around the base of plants are cues to browsing. Hence, percent removal includes both the amounts ingested and wasted.

Both plant biomass and percent removal were estimated on individual plants within plots by ocular calibration (Tadmor et al. 1975). Calibration trials were conducted each morning before data collection, and biomass and percent removed were visually estimated within the reference areas (Clark 1979).

Black-tailed jackrabbits are the only *Lepus* species in the lower elevations of Curlew Valley; although two cottontail species (*Sylvilagus nuttalli* and *Brachylagus idahoensis*) occur, they are scarce and restricted to habitats unlike the reference areas. Johnson (1961) surveyed food habits of rodents in similar Idaho rangeland and found that none ate significant amounts of *K. americana*, although it occurred in his study area. Hence, the observed browsing probably was nearly all by jackrabbits.

The second measure of jackrabbit use in the reference areas was the percentage of all *K. americana* plants within plots showing some utilization (Stoddart et al. 1975) and is hereinafter called "percent browsed." During the same months these measurements were made in the reference areas, similar percent-browsed observations were made on 100 *K. americana* plants along each of a number of transects randomly located through the Utah portion of Curlew Valley. Transects also were sampled in July 1981. Observed plants were selected by the wandering quarter method (Catana 1963).

Kochia americana density was measured in the reference areas in 1976 and 1980 with the 24 plots/exclosure as described; in summer 1981 at an exclosure, originally livestock- and jackrabbit-proof, established in 1957 by E. H. Cronin in about the center of the Utah portion of Curlew Valley; and at an exclosure termed CO4 by Rice and Westoby (1978) in the western part of the valley. At the Cronin exclosure, we placed 8 transects with a total of 121 0.1-m² quadrats each inside and outside, 6 m from and parallel to the fence. At CO4, we established 4 transects with a total of 40 0.2-m² quadrats each inside and outside, similarly oriented to the fence.

Unless otherwise noted, all plant means reported are accompanied by one standard deviation. Probability levels for all statistical

tests are the probability of a greater test statistic, assuming that the null hypothesis is true.

Jackrabbit Census

Jackrabbit populations in the Utah portion of Curlew Valley have been censused since fall 1962 as described in Gross et al. (1974). During the years of the present study, censuses were conducted by L. C. Stoddart (pers. comm.).

RESULTS

Historical Changes in *K. americana* Abundance

Early 1900s to 1950s-1970s

To our knowledge, the abundance of *K. americana* in salt-desert shrub vegetation of the eastern Great Basin at the time of European settlement was not recorded and is not known. Early explorers and settlers apparently lumped all salt-desert shrubs and half-shrubs in the single category "sage" or "sagebrush" (Christensen and Johnson 1964). Thus, although early reports describe the altitudinal distribution of shrub zones, it is not possible to distinguish the species and their abundance and distribution.

Nevertheless, several important accounts were recorded by the early 1900s. Kearny et al. (1914) presented a map of extensive (several km²), nearly monotypic *K. americana* zones in the vicinity of Tooele and Grantsville, Utah. Rogers (1980) reproduced photographs taken in 1912 in three areas of Tooele Valley showing similar monotypic stands. Cook (1961) inferred that such stands occurred in a mosaic with patches of sagebrush in Curlew Valley at some time preceding his observations in the late 1950s.

Kochia americana evidently declined in abundance between those early years and the decades of the 1950-1970s. Rogers (1980) photographed the original Shantz (Kearney et al. 1914) sites in Tooele Valley in 1978 and found former *K. americana* areas now occupied by exotic annuals and some weedy perennials (e.g., *Xanthocephalum sarothrae* and *Chrysothamnus nauseosus*). By the late 1950s, Cook (1961) found openings in sagebrush in Curlew Valley, which he inferred had previously been in *K. americana*, now largely covered with the exotic halogeton. Evidence of previous *K. americana* occupancy was provided by dead *K. americana* root crowns protruding from the soil surface. Similarly, in spring 1962, Dwayne Goodwin showed F. H. Wagner numerous dead root crowns in openings between sagebrush stands that were barren of live perennials. Thus, most of the decline probably occurred between early dates of abundance and the late 1950s.

Changes from 1950s to 1970s

Evidence of the past 24 years points to some further reduction during this period. When the Cronin enclosure was established in 1957, the *K. americana* density was comparable inside and outside the fence. In 1972, Westoby (1973) measured *K. americana* cover both inside and outside the enclosure and found it 25 times more abundant inside (0.25% vs. 0.01%). Today, a casual glance shows *K. americana* to be a common species inside the fence, but virtually nonexistent outside. In summer 1981 our measurements showed *K. americana* density at $3.5 \pm 9.9/\text{m}^2$ inside the same enclosure and $0.1 \pm 8.9/\text{m}^2$ outside (Table 1). Clearly *K. americana* has declined outside the enclosure in this area since 1957.

TABLE 1. Comparison of *K. americana* cover and density between 1972-73 and 1981 at two enclosures in Curlew Valley, Utah.

Enclosure and location	% cover \pm std. dev. (N)		Plants/m ² \pm std. dev. (N)	
	1972 ¹	1981 ²	1973 ¹	1981 ²
Cronin inside	0.25	2.5 \pm 6.6 (121)	—	3.5 \pm 9.9 (121)
Cronin outside	0.01	0.04 \pm 0.2 (121)	—	0.1 \pm 8.9 (121)
CO4 inside	0.8	1.2 \pm 2.7 (40)	2	4.7 \pm 10.0 (40)
CO4 outside	0.3	1.2 \pm 2.3 (40)	2	4.0 \pm 7.7 (40)

¹From Westoby (1973)

²This study

³From Rice and Westoby (1978)

Changes from 1971 to 1981

Several lines of evidence suggest that *K. americana* abundance may have reached a low point in the early 1970s and recovered in the last decade. The first is a comparison of standing-crop biomass measured in 1972 in several areas of Curlew Valley by Westoby (1973) with our own more recent measurements in the two reference areas. We estimated dry weight per live plant in late summer 1976, 1977, and 1980 (Table 2). The grand mean of 7.1 g/plant is 11.8 times the 0.6 obtained by Westoby (unpubl. data). Combining the density (Table 3) and dry-weight data for each area yields estimates of 16.0 ± 21.0 g/m² in the shadscale area, 6.0 ± 38.7 g/m² for the greasewood area. These values, more than 11.8 times the yearly average standing crop of 0.2 g/m² measured by Westoby (1973) in 1972 for his studied portions of the valley, imply greater density of plants and considerably greater standing crop. He estimated 2.4 g/m² average standing crop at the same greasewood site as the reference area in this study where we measured 6.0 g/m².

Secondly, in summer 1981, we estimated *K. americana* density and cover in the Cronin enclosure and Exclosure CO4, both measured 8–9 years earlier. The comparative figures (Table 1) show definite increase in both areas. Although Westoby (1973) considered the Cronin enclosure to be jackrabbit-proof in 1972, the fence is now perforated in several places and the interior accessible to rabbits. In 1981, as in 1973 (Rice and Westoby 1978), the fence around CO4 was not jackrabbit-proof and the interior subject to their use. Both are livestock-proof.

Changes from 1976 to 1980

Kochia americana density measurements in 1976 and 1980 (Table 3) suggest some slight

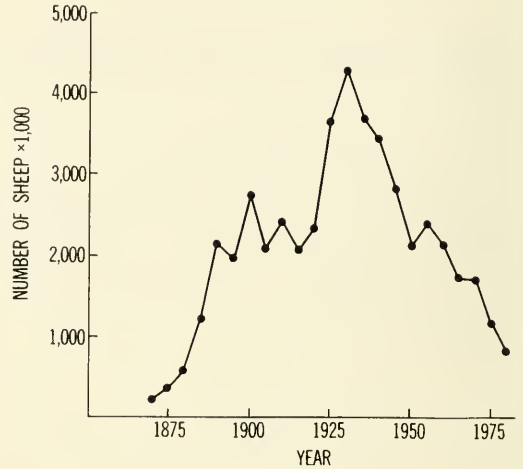


Fig. 1. Annual number of stock sheep plus lambs in Utah as reported by the USDA Statistical Reporting Service. Before 1924, only stock sheep were reported. Because the totals from 1925 to 1940 generally equaled 1.5–1.6 times the number of stock sheep, the latter values for 1870–1920 were multiplied by 1.5 to give the values in the graph.

decline in the two reference areas during the four-year period ($F=5.93$, $df=1,68$; $P=0.018$). Analysis of variance also showed the 2.6/m² in the greasewood area to be significantly greater than the 1.1/m² in the shadscale area ($F=53.32$; $df=1,68$; $P<0.001$), although dry-weight/plant (Table 2) was significantly less in the greasewood zone ($F=103.3$; $df=1,2$; $P<0.001$).

Changes in Herbivore Numbers

Sheep

Because the value of *K. americana* to live-stock generally is considered to be its use as winter sheep forage, only sheep numbers are considered here. USDA Statistical Reporting Service estimates of sheep numbers in Utah date back to 1870 and show a steady rise from low initial numbers to something over 2 million in 1890 (Fig. 1). They remained at

TABLE 2. Dry-weight biomass per live *K. americana* plant in two reference areas in Curlew Valley, Utah.

Sampling period	Mean biomass, g/plant ± 1 std. dev. (N)		
	Shadscale area	Greasewood area	Period means
September 1976	20.1 ± 35.1 (380)	2.3 ± 36.6 (931)	7.5 ± 36.2 (1311)
September 1977	8.4 ± 19.4 (311)	1.6 ± 20.1 (239)	5.4 ± 19.7 (550)
August 1980	12.8 ± 20.5 (151)	3.5 ± 8.7 (138)	8.4 ± 14.9 (289)
Area means	14.5 ± 26.7 (842)	2.3 ± 30.6 (1,308)	7.1 ± 19.1 (2,150)

about this level for the next 30 years, then rose to somewhere near 4 million between 1925 and 1940. Peak numbers were reached about 1930, and the industry declined thereafter. Numbers dropped below 1 million in the later 1970s, a level above which the industry had operated for nearly a century.

The records for Curlew Valley are not as complete, but Rice and Westoby (1978) have described several stages of livestock use in the valley that indicate declining grazing pressure from intensive use in 1869–1919 to the present. In this first half century, the area was a main travel route for herds driven to the railroad at its south end. This pressure disappeared in 1919 when the railroad was rerouted. Sheep and cattle grazing by local stockmen continued up to the present, but at declining levels, and today the grazing pressure probably is at the lowest level of a century or more. Present sheep grazing is confined to areas at least 15 km south of the locations where jackrabbit use of vegetation was estimated.

Jackrabbits

There has been a tendency in the small-mammal literature to consider black-tailed jackrabbits as seral animals that occur in greater numbers in disturbed areas (Vorhies and Taylor 1933, Phillips 1936, Smith 1940, Tiemeier 1965), although Flinders and Hansen's (1975) and MacCracken and Hansen's (1982) later findings do not follow the pattern. The tendency arising out of the earlier literature has been to assume that jackrabbits have increased since settlement as a result of grazing-induced vegetation changes (Taylor et al. 1935, Smith 1940, Taylor and Lay 1944).

Nevertheless, most of this theory comes from grassland (including desert grassland) regions. Jackrabbits evidently were quite abundant in the more arid West at settlement

time and before. Early settlers in what is now Utah recounted as early as 1860 large numbers of jackrabbits, in some cases decimating cultivated crops and serving as a dietary staple for Indian inhabitants (Christensen and Johnson 1964, Christensen and Hutchinson 1965). Palmer (1897) compiled a number of reports, some for northern Utah and southern Idaho, of high jackrabbit populations as early as 1854. One is from E. T. Seton for the Curlew Valley area in 1888. A number of accounts suggest pronounced population fluctuations.

First population measurements in northern Utah were begun in 1951 by Woodbury (1955) when populations were thought to have been at a cyclic peak. They declined during the 1950s, then recovered to another in 1959 measured by French et al. (1965) in southern Idaho. This high occurred about 1960 in Curlew Valley (Currie and Goodwin 1966, Gross et al. 1974). Since then, jackrabbit populations have been censused annually in Curlew Valley, the approximate 10-year cycle peaking in 1970 and again in 1980 (Fig. 2).

The long-term trend on which this 10-year periodicity is superimposed can only be speculated on. Early accounts suggest densities greater than what we experience today (Christensen and Johnson 1964), and a long-term trend in abundance that is generally downward (French and Heasley 1981).

Subjectively, the 1970 high seemed to be lower than the 1959–1960 high to those of us who had witnessed both. And the censuses in Curlew Valley clearly show the 1980 peak to have been about twice that of 1970.

In total, early densities seem to have been high and may have declined somewhat in the present century, perhaps to a low point in the 1960s and 1970s. Whether or not the higher numbers of the 1979–1981 peak portend a reversal of the trend remains to be seen.

TABLE 3. Density of *K. americana* at two reference areas in Curlew Valley, Utah.

Sampling period	Mean density, plants/m ² ± std. dev. (N)		
	Shadscale area	Greasewood area	Period means
May 1976	1.2 ± 0.9 (24)	2.8 ± 1.1 (24)	2.0 ± 1.0 (48)
August 1980	0.8 ± 0.4 (12)	2.1 ± 0.7 (12)	1.5 ± 0.6 (24)
Area means	1.1 ± 0.7 (36)	2.6 ± 1.0 (36)	1.8 ± 0.9 (72)

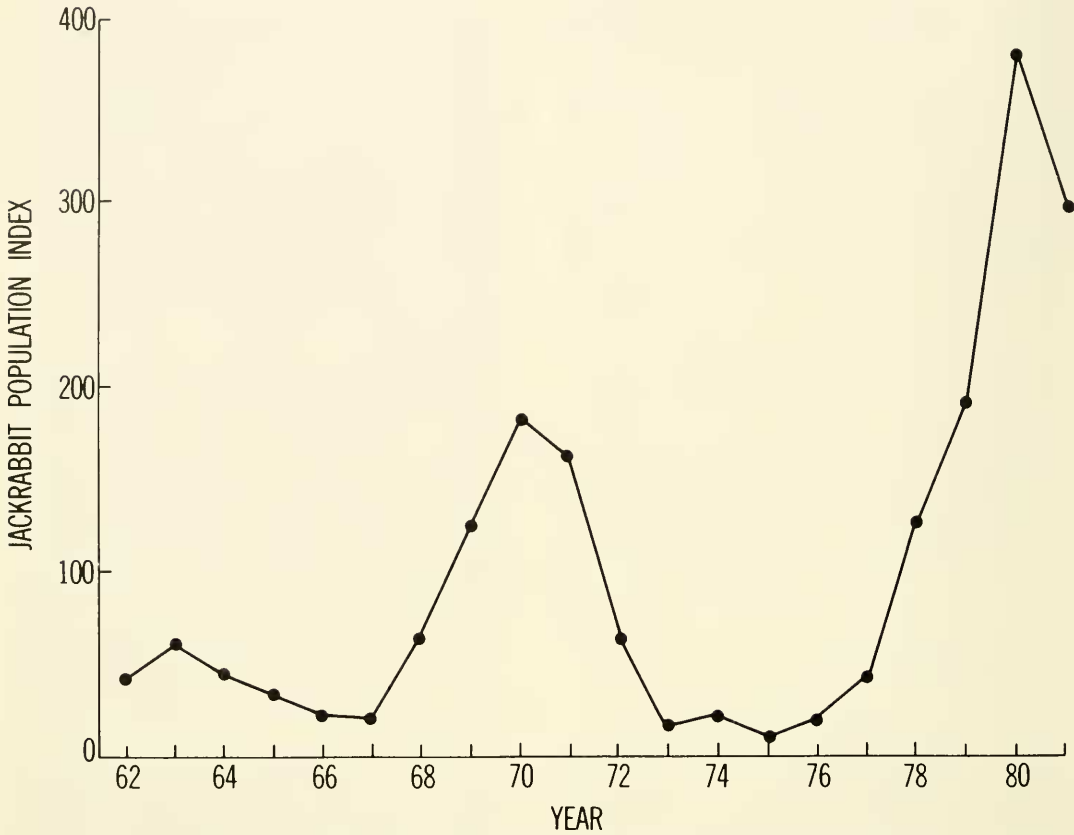


Fig. 2. Indices of black-tailed jackrabbit population density in Curlew Valley, northwestern Utah. Census method is described in Gross et al. (1974), and the data are from L. C. Stoddart (pers. comm.).

Jackrabbit Impacts on *K. americana*

Effects on Individual Plants

The percentage of aboveground phytomass removed from individual *K. americana* plants (Table 4) seems to increase progressively from early summer, at the time of peak standing crop, to midwinter. This is expected, both because the rabbit population increases during the summer from reproduction and because fewer foods are available in winter (Clark 1979), so rabbits browse for a longer time on a selected plant.

By the end of summer, when the plants were lignifying, rabbits had removed from 33% to 50% of the phytomass on browsed plants in the three years of observation. By February 1977 and 1978, two low rabbit

years, these values had risen to somewhere between 45% and 82% by the end of winter.

Similarly, Currie and Goodwin (1966) noted that jackrabbits remove a large proportion of herbage from individual plants when

TABLE 4. Percentage of herbage removed by jackrabbits from individual *K. americana* plants on two reference areas in Curlew Valley, Utah.

Sampling period	Mean % removed/ plant \pm std. dev. (N)	
	Shadscale area	Greasewood area
June 1976	10.9 \pm 4.9 (6)	18.9 \pm 6.6 (6)
September 1976	31.0 \pm 17.8 (29)	47.2 \pm 37.1 (164)
February 1977	64.9 \pm 65.1 (49)	81.7 \pm 11.1 (3)
June 1977	13.2 \pm 2.7 (2)	11.0 \pm - (1)
September 1977	42.2 \pm 15.5 (13)	48.4 \pm 11.7 (22)
February 1978	45.9 \pm 19.5 (105)	45.6 \pm 3.7 (8)
August 1980	37.7 \pm 16.1 (22)	32.3 \pm 15.8 (15)

they select one they prefer during a feeding period. Occasionally, they clip off small shrubs, such as *K. americana*, at ground level. In September 1981, *K. americana* plants were actually dug out of the ground, apparently to chew the root crown and cambium around the base of the stem. In 20 1-m² quadrats placed at 3-m intervals along a transect immediately west of the greasewood reference area, 11 of 93 plants (12%) had been dug out and partly eaten.

Mean percentage of herbage removed from plants in the greasewood area ($46.2 \pm 32.7\%$) in August–September of the three years (Table 4) was significantly greater than that ($35.6 \pm 16.7\%$) removed in the shadscale area ($F=5.75$; $df=1,2$; $P=0.018$). This may have been due to the smaller stature of the plants in the greasewood area (Table 2).

We tested the null hypothesis that the August–September percentages for the three years were equal and found no significant differences ($F=1.89$; $df=2,2$; $P=0.346$). As jackrabbit density increases, as occurred from 1976 to 1981 (Fig. 2), one might expect more intense browsing on individual plants of this preferred species, but that was not the case in these years. Although individual plants may be heavily used, jackrabbits often skip over adjacent plants seemingly similar to those browsed.

If any between-year variation occurred, it was inversely correlated with the annual variations in biomass/plant, although the yearly means shown in Table 2 were not statistically different ($F=0.1$; $df=2,2$; $P=0.999$). Yearly variations in the dry weight of half-shrubs

such as *K. americana* probably are related to variations in precipitation (West and Fareed 1973).

Percentage of Plants Browsed

Like the percent removal, the percentage of plants browsed appears to increase from June to February (Table 5). This trend is clear for the shadscale area in both years and for the valleywide transects in 1977–1978. In these areas, percent browsed rose from about 1%–3% in June to about 4%–8% in September of the low rabbit years 1976 and 1977, and to 8.4% by February of these same years. The progressive increase in percent browsed, also like percent removal, would be expected to be a cumulative parameter both as the rabbit population increased through the summer and as an increasing fraction of the plants were selected and fed upon.

In 1980 and 1981, at peak rabbit population, measured late-summer percentages in the shadscale and transect areas were 15%–21%. Because no winter measurements were made in these years, the final percentage of plants browsed before the next growing season was undoubtedly higher. Furthermore, the late-summer digging described probably increased further the percentage of plants affected by rabbits, unless for some reason (e.g., palatability) the digging was confined to already-browsed plants.

The percent browsed increased from June to September in the greasewood reference area, as in the other areas, but then declined from September to February. Inasmuch as measurements were restricted to freshly

TABLE 5. Percentage of *K. americana* plants browsed by jackrabbits on two reference areas and valleywide transects in Curlew Valley, Utah.

Sampling period	Mean % browsed \pm std. dev. (N) ¹		
	Shadscale area	Greasewood area	Transects
June 1976	1.2 \pm 0.4 (12)	1.1 \pm 0.4 (24)	—
September 1976	7.6 \pm 1.4 (24)	17.7 \pm 1.3 (24)	—
February 1977	13.8 \pm 1.8 (24)	1.0 \pm 0.6 (24)	—
June 1977	0.7 \pm 0.5 (24)	0.4 \pm 0.4 (24)	3.1 \pm 3.0 (14)
September 1977	4.2 \pm 1.1 (24)	9.2 \pm 1.9 (24)	5.8 \pm 4.3 (12)
February 1978	38.6 \pm 3.0 (24)	3.8 \pm 1.9 (24)	7.9 \pm 5.1 (7)
August 1980	14.6 \pm 2.9 (12)	10.9 \pm 2.7 (12)	15.3 \pm 6.9 (10)
July 1981	—	—	21.4 \pm 11.6 (12)

¹No. of quadrats for reference areas, no. of transects valleywide

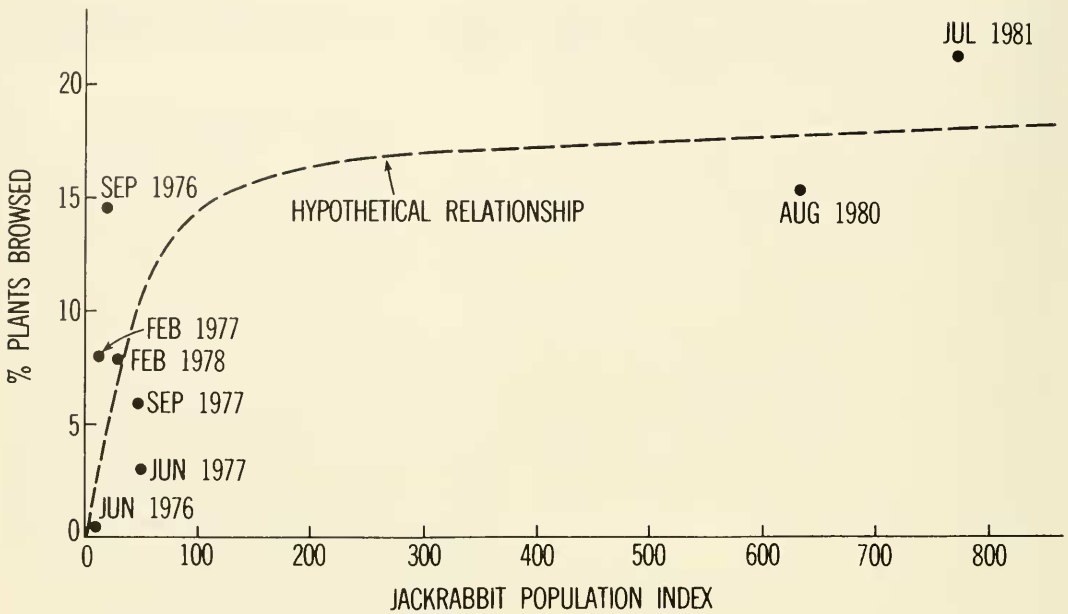


Fig. 3. Relationship between percentage of *K. americana* browsed by jackrabbits and jackrabbit population index in Curlew Valley, Utah. The points for 1976 are from the reference areas only; the remaining points are from transects throughout the valley.

browsed plants, the explanation probably lies in the high density (Table 3) of *K. americana* within the greasewood area. During 1976–1978, many small (<1.0 g/plant) *K. americana* plants sprouted from old root crowns in the spaces between the greasewood. These small plants were largely ignored by rabbits, especially in the winter when they were drier than larger, more robust plants. Because feeding by rabbits is patchy, varying with plant condition, plant density, and habitat, the transects that were located in a variety of areas probably are the best indicators of valleywide patterns.

To explore further the question of whether the percentage of plants browsed by jackrabbits increases as they increase, we tested the null hypothesis that the August–September percentages were the same at both reference areas between years (Table 5). We concluded that the percent browsed did differ significantly between years ($X^2=28.04$; $df=3$; $P<0.001$).

Because the reference areas are only a small part of Curlew Valley, we also tested, with data from the transects, the hypothesis that dense populations browse a larger percentage of the *K. americana* plants (Table 5).

Mean percentage of plants browsed on transects in September 1977, August 1980, and July 1981 is significantly different when compared by a Kruskal-Wallis test ($X^2=14.64$; $df=2$; $P=0.001$; Sokal and Rohlf 1969:388–390). Thus, on the basis of evidence from both reference areas and transects, higher rabbit populations do affect more *K. americana* plants.

On the basis of empirical evidence, Clark (1979) predicted that if the relationship between *K. americana* use and jackrabbit density were linear, 90% of all *K. americana* plants would be browsed during the highest population periods. Westoby (1974), on the basis of more theoretical arguments, concluded that preferred, palatable, and rare plants such as *K. americana* would be under severe browsing pressure from rabbits. To test these predictions, we examined the relationship between percentage of plants browsed and the jackrabbit population index by using all occasions for which we had measurements of both variables (Fig. 3). Although the figure is sketchy, it suggests a curvilinear relationship, not a linear one. Even at the highest rabbit population levels recorded in two decades (Fig. 2), only about 20% of the

plants were browsed by late summer. By regressing percent browsed (Y) on the logarithm of jackrabbit population index (X), we produced an adequate equation to predict what browsing levels would be under extremely high populations ($F=6.69$; $df=6$; $P=0.04$; $r=0.73$). $Y = -2.06 + 2.94 X$.

At the highest population levels for which we had data on percent browsed, the relationship predicts mean utilization of about 17%, with 95% confidence limits of approximately 2%–33%. Because it is possible that historical rabbit population levels were much higher, we made a similar prediction for a population index of 1550, twice as abundant as our highest observed levels. Predicted mean percent browsed was only 20%, with 95% confidence limits of approximately 3%–36%. Even at the highest population levels, percent browsed by rabbits does not even approach 100% of the *K. americana* plants.

DISCUSSION AND CONCLUSIONS

Kochia americana was an abundant species in the salt-desert shrub vegetation of the eastern Great Basin in the early 1900s and, we suspect, as early as European settlement. The species declined sharply in this century in the areas of nearly pure stands, as shown by the photographic evidence and the dead root-crown remains seen as late as the early 1960s. Whether or not its density declined in those areas where it coexists with shadscale or greasewood is unknown. The evidence suggests an increase in *K. americana* abundance in these types since the early 1970s, much as it is increasing in the openings where it formerly occurred in pure stands.

Why the species declined so sharply is a matter of speculation, but we suspect that the primary stimulus was grazing livestock, primarily sheep. The view that livestock numbers built up to historically high numbers and that the major changes in range vegetation occurred before 1900 is encountered in the range literature. But sustained, maximum numbers of both sheep and cattle did not build up in the West until well into the 20th century (Wagner 1978).

In Utah, sheep numbers did not rise well above 2 million until 1900, and then they remained above this level for more than half a

century (Fig. 1). Peak numbers were reached in about 1930. If the area under the curve in Fig. 1 is taken as the total sheep-grazing pressure on Utah ranges since settlement, then only about 16% was incurred from 1870 to 1900, whereas about 63% was applied from 1900 to 1950.

Black-tailed jackrabbits were abundant in Utah at settlement time, as was *K. americana*. Hence, its decline probably was not primarily induced by rabbit browsing, with which it had long coexisted. However, jackrabbit browsing may have added to the sheep pressure, providing a collective effect that was more than *K. americana* could sustain, and together they may have caused its shrinkage. Nevertheless, livestock was likely the major new variable that elicited the decline.

The hypothesis that livestock browsing, with or without jackrabbit pressure, was responsible for the decline in Curlew Valley, and not some other influence such as insects, disease, or weather, is supported by the enclosure data (Table 1). *Kochia americana* virtually disappeared outside the Cronin enclosure after 1957, but maintained a healthy stand inside. And, although the differences are not statistically significant, mean percent *K. americana* cover and density were greater inside Enclosure CO4 (established in 1956) than outside, both in Rice and Westoby's (1978) measurements in 1973 and ours in 1981.

A jackrabbit influence may be suggested by these results. The Cronin enclosure was jackrabbit-proof at least through 1972 (Westoby 1973). Jackrabbit protection in CO4 lapsed after 1969 (Rice and Westoby 1978). Perhaps significantly, the inside-outside difference is much more marked in the Cronin plot than in CO4 (Table 1).

The livestock influence may be inferred both from the *K. americana* decline during high sheep numbers and from the *K. americana* increase since the early 1970s, when sheep numbers have been profoundly reduced but jackrabbit grazing has continued. Parenthetically, the *K. americana* increase is contrary to Westoby's (1973, 1981) contention that the species could not recover because of salt deposition on the soil surface by halogeton.

The available data provide a closer look at the jackrabbit influence. Westoby (1973) concluded that *K. americana* was highly preferred by jackrabbits, whereas Clark (1979, 1981) found it only moderately preferred. Nevertheless, both investigators found the species a relatively minor dietary component.

At high rabbit density, and perhaps the low point of *K. americana* abundance in early 1972, Westoby calculated virtually complete utilization by the end of the year on the basis of known consumption rates, dietary composition, and estimated *K. americana* standing crop. Our own direct measurements of percent browsed show much lower rates in the low rabbit years of 1976 and 1977 (Table 5) and when *K. americana* evidently was more abundant than during Westoby's measurements. These are the expected results if *K. americana* has increased since the early 1970s: utilization rate is a positive function of the number of plants consumed per herbivore and the number of herbivores, and a negative function of the number of plants. Both a decrease in number of herbivores and an increase in the number of plants will tend to reduce the utilization rate.

Our measurements indicate somewhat higher late summer percentage of plants browsed in the high rabbit years of 1980 and 1981 (Table 5), although these are still lower than Westoby's estimate of total utilization. But, because his were calculated for year-long use and we did not make winter measurements in these two years, the two sets of rates may not be entirely comparable, nor can we say what the final, year-long utilization levels were in 1980 and 1981. Our data show 45%–82% removal of herbage from browsed plants by February of 1976 and 1977 (Table 4), both low rabbit years. We do not know what level of browsing an individual *K. americana* plant can sustain, although small plants can easily be destroyed by browsing jackrabbits. But even the percent removal of the low years, applied to an appreciable fraction of *K. americana* plants in high rabbit years, would seem to be a significant impact. If rabbit browsing during cyclic highs were intensive enough to kill an appreciable fraction of *K. americana* plants, this could produce variations in plant density. However, we can infer from our regression

and the present abundance of *K. americana* that the year-long percentage of plants browsed has not reached 100%.

Collectively, the data suggest the following hypothetical scenario. *Kochia americana* was abundant in the salt-desert shrub vegetation of the eastern Great Basin up to the early 1900s in the presence of large jackrabbit populations, but under no, then initially moderate, livestock use. Between the early 1900s and the early 1970s it declined broadly, then appears to have increased in the 1970s and early 1980s. This general trend probably was induced by heavy livestock pressure in the first half of the century, then reduction of the pressure in the third quarter. The decline may have been abetted by jackrabbit browsing, but the recovery is occurring in the face of that browsing.

The sequence for Curlew Valley may have differed slightly because of its location as a livestock shipping route and the possibility of earlier livestock pressure. But, given the *K. americana* root crowns as late as 1962 and comparable density inside and outside Cronin's enclosure in 1957, its abundance evidently persisted well into the first half of this century.

Much more hypothetically, some short-term cyclic variation in *K. americana* abundance may be superimposed on the broad trend by cyclic jackrabbit pressure—at least in the middle of the century when *K. americana* was scarce in comparison with the early 1900s—and the ratio of jackrabbit herbivory to *K. americana* abundance may be higher than under pristine conditions. This hypothetical scenario needs to be tested with long-term, annual concurrent measurement of *K. americana* and jackrabbit densities.

ACKNOWLEDGMENTS

The authors thank L. C. Stoddart for unpublished data on jackrabbit populations from research supported by the U.S. Department of Energy, Contract E(11-1)-1329. The study was also supported in part by NSF Grant 15886 for the US/IBP Desert Biome and by Iowa State University; Journal Paper J-10797 of the Iowa Agriculture and Home Economics Experiment Station, Ames. Project 2401.

LITERATURE CITED

- CATANA, A. J. 1963. The wandering quarter method of estimating population density. *Ecology* 44:349-360.
- CHRISTENSEN, E. M., AND H. B. JOHNSON. 1964. Pre-settlement vegetation and vegetational change in three valleys of central Utah. *Brigham Young Univ. Sci. Bull., Biol. Ser.* 4(4): 16 pp.
- CHRISTENSEN, E. M., AND M. A. HUTCHINSON. 1965. Historical observations on the ecology of Rush and Tooele valleys, Utah. *Proc. Utah Acad. Sci., Arts, Lett.* 42:90-105.
- CLARK, W. R. 1979. Population limitation of jackrabbits: an examination of the food hypothesis. Unpublished dissertation. Utah State Univ., Logan. 242 pp.
- . 1981. Role of black-tailed jackrabbits in a North American shrub-steppe ecosystem. Pages 706-719 in K. Myers and C. MacInnes, eds., *Proceedings World Lagomorph Conference*, Aug. 1979, Guelph, Ontario. 983 pp.
- CLARKE, L. D., AND N. E. WEST. 1969. Germination of *Kochia americana* in relation to salinity. *J. Range Manage.* 22:286-287.
- COOK, C. W. 1961. Seeding response and soil characteristics on adjacent sagebrush and desert molly soils. *J. Range Manage.* 14:134-138.
- COOK, C. W., AND L. A. STODDART. 1953. The halogeton problem in Utah. *Utah Agric. Exp. Sta. Bull.* 364. 44 pp.
- CURRIE, P. O., AND D. W. GOODWIN. 1966. Consumption of forage by black-tailed jackrabbits on salt-desert ranges of Utah. *J. Wildl. Manage.* 30:304-311.
- ELLISON, L. 1960. Influence of grazing in plant succession of rangelands. *Bot. Rev.* 26:2-66.
- ESPLIN, A. C., J. E. GREAVES, AND L. A. STODDART. 1937. A study of Utah's winter range: composition of forage plants and use of supplements. *Utah Agric. Expt. Sta. Bull.* 277. 48 pp.
- FLINDERS, J. T., AND R. M. HANSEN. 1975. Spring population responses of cottontails and jackrabbits to cattle grazing shortgrass prairie. *J. Range Manage.* 28:290-293.
- FRENCH, N. R., AND J. E. HEASLEY. 1981. Lagomorphs in the shortgrass prairie. Pages 695-705 in K. Myers and C. MacInnes, eds., *Proceedings World Lagomorph Conference*, Aug. 1979, Guelph, Ontario. 983 pp.
- FRENCH, N. R., R. McBRIDE, AND J. DETMER. 1965. Fertility and population density of the blacktail jackrabbit. *J. Wildl. Manage.* 29:14-26.
- GROSS, J. E., L. C. STODDART, AND F. H. WAGNER. 1974. Demographic analysis of a northern Utah jackrabbit population. *Wildl. Monogr.* 40. 68 pp.
- HOLMGREN, R. C., AND S. S. HUTCHINGS. 1972. Salt desert shrub response to grazing use. Pages 153-164 in C. M. McKell, J. P. Blaisdell, and J. R. Goodin, eds., *Wildland shrubs—their biology and utilization*. USDA For. Serv. Tech. Rep. INT-1. 494 pp.
- JOHNSON, D. R. 1961. Food habits of rodents on rangelands of southern Idaho. *Ecology* 42:407-410.
- KEARNY, T. H., L. J. BRIGGS, H. L. SHANTZ, J. W. McLANE, AND R. L. PIEMEISEL. 1914. Indicator significance of vegetation in Tooele Valley, Utah. *J. Agric. Res.* 1:365-417, maps and photos.
- MACCRACKEN, J. G., AND R. M. HANSEN. 1982. Herbaceous vegetation of habitat used by blacktail jackrabbits and Nuttall cottontails in southeastern Idaho. *Amer. Midl. Nat.* 107:180-184.
- PALMER, T. S. 1897. The jack rabbits of the United States. USDA Div. Biol. Surv. Bull. 8. 88 pp.
- PHILLIPS, P. 1936. The distribution of rodents in overgrazed and normal grasslands in central Oklahoma. *Ecology* 17:673-679.
- RICE, B. L., AND M. WESTOBY. 1978. Vegetation responses of some Great Basin shrub communities protected against jackrabbits or domestic stock. *J. Range Manage.* 31:28-34.
- ROGERS, G. F. 1980. Photographic documentation of vegetation changes in the Great Basin Desert. Unpublished dissertation. Univ. of Utah, Salt Lake City. 160 pp.
- SHINN, R. S., R. D. ANDERSON, M. MERRITT, W. OSBORNE, AND J. A. MACMAHON. 1975. Curlew Valley validation site report. USIBP Desert Biome Res. Memo. RM 75-1. Utah State Univ., Logan. 68 pp.
- SHOEMAKER, V. H., K. A. NAGY, AND W. R. COSTA. 1976. Energy utilization and temperature regulation by jackrabbits (*Lepus californicus*) in the Mojave Desert. *Physiol. Zool.* 49:364-375.
- SMITH, C. C. 1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. *Ecology* 21:381-397.
- SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman Co., San Francisco. 776 pp.
- STEWART, G., W. P. COTTAM, AND S. S. HUTCHINGS. 1940. Influence of unrestricted grazing on northern salt desert plant associations in western Utah. *J. Agric. Res.* 60:289-316.
- STODDART, L. A., A. D. SMITH, AND T. W. BOX. 1975. *Range Management*. 3d ed. McGraw-Hill Book Co., New York. 532 pp.
- TADMOR, N. H., A. BRIEGHET, I. NOY-MEIR, R. W. BENJAMIN, AND E. EVAL. 1975. An evaluation of the weight-estimate method for measuring production in annual vegetation. *J. Range Manage.* 28:65-69.
- TAYLOR, W. P., C. T. VORHIES, AND P. B. LISTER. 1935. The relation of jack rabbits to grazing in southern Arizona. *J. For.* 33:490-498.
- TAYLOR, W. P., AND D. W. LAY. 1944. Ecologic niches occupied by rabbits in eastern Texas. *Ecology* 25:120-121.
- TIEMEIER, O. W. 1965. Bionomics. Pages 5-37 in *The black-tailed jackrabbit in Kansas*. Kansas Agric. Expt. Sta. Tech. Bull. 140. 75 pp.
- VORHIES, C. T., AND W. P. TAYLOR. 1933. The life histories and ecology of jackrabbits, *Lepus alleni* and *Lepus californicus* spp., in relation to grazing in Arizona. *Univ. Arizona Agric. Expt. Sta. Tech. Bull.* 49. 117 pp.
- WAGNER, F. H. 1978. Livestock grazing and the livestock industry. Pages 121-145 in H. P. Brokaw, ed., *Wildlife and America: contributions to an understanding of American wildlife and its conservation*. U.S. Coun. Environ. Qual., U.S. Fish Wildl. Serv. U.S. For. Serv., U.S. Nat. Ocean. Atmos. Admin. 532 pp.

- WEST, N. E., AND M. FAREED. 1973. Shoot growth and litter fall processes as they bear on primary production of some cool desert shrubs. USIBP Desert Biome Res. Memo. RM 73-9. Utah State Univ., Logan. 13 pp.
- WESTOBY, M. 1973. Impact of black-tailed jackrabbits (*Lepus californicus*) on vegetation in Curlew Valley, northern Utah. Unpublished dissertation, Utah State Univ., Logan. 164 pp.
- . 1974. An analysis of diet selection by large generalist herbivores. *Amer. Nat.* 108:290-304.
- . 1980. Black-tailed jackrabbit diets in Curlew Valley, northern Utah. *J. Wildl. Manage.* 44:942-948.
- . 1981. Elements of a theory of vegetation dynamics in arid rangelands. *Israel J. Bot.* 28:169-194.
- WOODBURY, A. M. 1955. Ecology of the Great Salt Lake desert. I. An annual cycle of the jackrabbit. *Ecology* 36:353-356.